
TAXONOMIC REVISION OF THE GENUS SARCOLAENA (SARCOLAENACEAE)¹

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ABSTRACT

A systematic study, based primarily on morphology, suggests that patterns of variation in *Sarcolaena* Thouars, a member of the Malagasy endemic family Sarcolaenaceae, are best resolved by recognizing eight species. Keys for identification of the genera of Sarcolaenaceae and species of *Sarcolaena* are provided, as well as a discussion of the overall morphology of *Sarcolaena* and complete descriptions of its species. Two species, *S. grandiflora* and *S. multiflora*, are lectotypified in the present study.

Madagascar is the world's fourth largest island with a land area of approximately 590,000 km². Lying in the Indian Ocean about 400 km southeast of the African mainland, it extends 1650 km from 12° to 25° latitude south (Griffiths & Ranaivoson, 1972). Madagascar the island separated from the African coastline more than 100 million years ago (Rabinowitz et al., 1983). However, debate about its paleoposition before the breakup of Gondwanaland still continues. According to Rabinowitz et al. (1983), Madagascar was attached to Africa along the Somalian, Kenyan, and Tanzanian coastlines. A more recent study of the paleomicroflora of Tanzania and Madagascar by Hankel (1993) suggested that Madagascar was contiguous with Africa further south, along the southeast Kenya, Tanzania, and northern Mozambique coasts.

Since its separation from the African mainland, Madagascar has been the center of tremendous evolutionary diversification. Madagascar's wide range of habitats and its long geographic isolation have resulted in unusually high levels of endemism of plants and animals. Its unique flora has resulted from the persistence of relic taxonomic groups associated with the process of numerous localized speciation events, a phenomenon often observed in continental islands (Whittaker, 1999). Although Madagascar has a varied and rich flora, unfortunately it is poorly characterized and, most frustrating of all, some species of plants will disappear before they are even known scientifically. Estimates

of the size of the flora and levels of endemism vary widely. Phillipson (1994) suggested that the known Malagasy flora has 9345 species, of which 7581 (81%) are endemic. Lowry (1992) estimated that 75% of the 10,000 to 12,000 native species found in Madagascar are endemic. Perrier de la Bathie (1936) estimated 20% of the 1289 plant genera were endemic. Despite modern taxonomic revision for some families and many descriptions of new species, inadequate taxonomic treatments for most of the flora continue to prevent more precise estimates of its size and levels of endemism.

The largest of the endemic families in Madagascar is Sarcolaenaceae, which consists of eight to ten genera and about 34 species. Within Sarcolaenaceae, one of the larger genera is *Sarcolaena* with eight species recognized here, one of which is recently described (Randrianasolo & Miller, 1994). The genus is well defined within the family by morphological characters such as prefoliation traces on leaf surfaces and ovary locules each containing only two ovules. However, limits among its species have been poorly defined in previous taxonomic studies. The present study incorporates new characters from morphology to address specific limits in *Sarcolaena*. The number of specimens available for study has increased greatly since the last monograph (Cavaco, 1952a), permitting much better assessment of character variability within and between species.

The goal of the present study is to resolve spe-

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Table 1. List of morphological characters and character states used to delimit *Sarcolaena* species.

Characters	Character states
1. Tree height	
2. Leaf	
a—size	
b—blade shape	lanceolate/narrowly ovate or elliptic/ovate/oblanceolate/obovate
c—indumentum	glabrous/pubescent
d—apex shape	acute/acuminate/attenuate/mucronate/retuse/obtuse
e—base shape	acute/cuneate/obtuse/rounded/subcordate
3. Inflorescence	
a—position	terminal/axillary
b—flower number	
4. Involucre	
a—shape	widely ovoid/very widely ovoid
b—size at floral and fruit stage	
c—indumentum	sericeous/setaceous/hirsute/spreading
5. Flower	
a—sepal number	3/5
b—sepal shape	ovate/widely ovate/very widely ovate/widely depressed ovate
c—petal size	
d—petal color	white/yellow
e—stamens number	
f—ovary size	
g—style length	
h—style indumentum	glabrous/pubescent
6. Fruit	
a—size	
b—enclosure in the involucre	partial/complete

cies delimitation within *Sarcolaena*, to clarify nomenclatural problems, including lectotypification of taxa, where necessary and appropriate, and to generate a complete monographic treatment for the genus. Parallel descriptions of species, as well as a key for their identification, are provided.

MATERIALS AND METHODS

Over 200 herbarium specimens were examined, with additional collections made during field studies from 1992 to 1993 in Madagascar. To understand the variation within individuals and also within and among populations, 5–10 individuals from 2–5 populations were sampled for each plant species when feasible. For each of these, 3 different collection numbers were made, distributed from the top, center, and bottom of tree crowns. Fresh buds in varying developmental stages as well as flowers were collected and preserved in formalin/acetic acid/ethanol (FAA) (Radford et al., 1974) to supplement material available from herbarium specimens. Ecological and edaphic data were compiled

from both literature and herbarium labels and were supplemented with field observations.

A series of morphological characters were measured and recorded for each specimen (Table 1). Continuously ranging characters such as leaf length or width were measured and recorded. Qualitative characters, such as shape, form, position, or texture, conform to Radford et al. (1974) and Hickey (1973).

SYSTEMATICS OF SARCOLAENACEAE

The Sarcolaenaceae are the largest of ten angiosperm families endemic to Madagascar (Takhtajan, 1997; Table 2). The family is concentrated in the eastern and central regions of Madagascar. A few genera reach the Sambirano region in the northwest, which is similar climatically to the east, but very few members occur in the western region.

The family consists of trees or shrubs with alternate, simple, entire, persistent and stipulate leaves. Most species have terminal or axillary cymose inflorescences, which are less commonly corymbiform

Table 2. Endemic vascular plant families in Madagascar.

Family	Number of genera	Number of species
Sarcolaenaceae	10	35
Sphaerosepalaceae	2	17
Didieraceae	4	11
Melanophyllaceae	1	8
Kaliphoraceae	1	1
Didymelaceae	1	2
Physenaceae	1	2
Bembiciaceae	1	1
Diegodendraceae	1	1
Asteropeiaceae	1	1

or paniculiform, or occasionally solitary flowers. Flowers are perfect and regular, with 3 to 5 sepals and 5 to 6 petals. The number of stamens varies from 5 to 100, and the ovary is superior and has 2 to 5 locules. An involucre is present, and a nectariferous disk is sometimes present in a flower between stamens and petals.

NOMENCLATURAL HISTORY

The first description of species of Sarcolaenaceae, originally known as Chlaenaceae, was made by Aubert Du Petit-Thouars (1806). The original family description included four genera with two common characters: the presence of 3 sepals and an involucre covering the flower. The original familial name Chlaenaceae refers to this involucre, using the Greek *chlaina* or *laena*, meaning superior or exterior tunic. Other names proposed after Chlaenaceae include Sarcolaenaceae Caruel (1881) and Rhodolaenaceae Bullock (1957), of which Sarcolaenaceae was conserved (Greuter et al., 1994). Since Thouars's publication in 1806, six additional genera were subsequently described in the family. Baker (1882) described *Xerochlamys* with its dry involucre, numerous stamens, and ovary containing 2 to 4 ovules per locule. Two genera, *Xyloolaena* and *Eremolaena*, were added by Baillon in 1879 and 1884, respectively. *Pentachlaena*, with its involucre reduced to 4 or 5 bracts subtending two sessile flowers each with a large disk and unequally sized and free stamens, was described by Perrier de la Bâthie (1920). Recently, *Perrierodendron* was described by Cavaco (1952c) based essentially on its ovary and fruit characters. Finally, *Mediusella* was segregated from *Leptolaena* by Hutchinson in 1973 (Table 3). *Sarcolaena* Thouars was chosen as the type genus of the family (Greuter et al., 1994).

Table 3. Genera of Sarcolaenaceae with number of species recognized by Cavaco (1952a) and Capuron (1970).

Genera	Number of species	
	Cavaco	Capuron
<i>Sarcolaena</i> Thouars (1806)	7	7
<i>Leptolaena</i> Thouars (1806)	7	2
<i>Rhodolaena</i> Thouars (1806)	4	4
<i>Schizolaena</i> Thouars (1806)	8	9
<i>Xyloolaena</i> Baillon (1879)	3	3
<i>Xerochlamys</i> Baker (1882)	0	4
<i>Eremolaena</i> Baillon (1884)	2	2
<i>Pentachlaena</i> P. de la Bâthie (1920)	1	2
<i>Perrierodendron</i> Cavaco (1952c)	1	1
<i>Mediusella</i> (Cavaco) Hutch. (1973)	0	1

FOSSIL RECORD

According to Emberger (1944), Sarcolaenaceae originated from the Theales during the Cretaceous period (from 141 to 65 MYA), and species were probably widespread throughout Gondwanaland. His hypothesis was later supported by the finding of *Xyloolaena*-type pollen of estimated lower Miocene age from the Cape region of South Africa (Coetzee & Muller, 1984). The occurrence of Sarcolaenaceae outside of Madagascar would indicate that the current endemic distribution on Madagascar results from extinction on mainland Africa rather than its independent origin and adaptive radiation on the isolated island landmass after its mainland separation.

SYSTEMATIC POSITION OF SARCOLAENACEAE

The relationships and systematic positioning of Sarcolaenaceae have been unclear. The wide diversity of opinions on the relationships of Sarcolaenaceae has included placement in Theales (Hutchinson, 1926; Cronquist, 1981), Ochnales (Hutchinson, 1973), or Malvales (Heywood, 1978; Takhtajan, 1980; Dahlgren, 1983) (Table 4). The presence of imbricate sepals suggests placement in the Theales. However, the presence of mucilage cells, stratified secondary phloem in the cortex (Outer & Vooren, 1980), as well as malvalic and sterculic cyclopropene fatty acids (Gaydou & Ramanolima, 1983) are all characters allying with Malvales. Molecular study based on *rbcL* and *atpB* sequences strongly suggests that Sarcolaenaceae belong to an expanded malvaceous clade (Alverson et al., 1998; Bayer et al., 1999).

Table 4. Affinities of the Sarcolaenaceae.

Characters	References	Indicated affinity
Secondary phloem	Outer & Vooren (1980)	Malvales
Secondary xylem	Outer & Schutz (1981)	Malvales
Pollen morphology	Takhtajan (1983)	Malvales
Petiolar anatomy	Takhtajan (1983)	Malvales
Fatty acids	Gaydou & Ramanoelina (1983)	Malvales
Vessel length & diameter	Hutchinson (1973)	Ochnales
Sepals aestivation	Cronquist (1981)	Theales
<i>rbcL</i> sequence data	Alverson et al. (1998)	Malvales
<i>atpB</i> sequence data	Bayer et al. (in press)	Malvales

GENERIC RELATIONSHIPS

Cavaco (1952a) recognized 8 genera and 33 species in Sarcolaenaceae. Capuron (1970) proposed 10 genera with 35 species for the family, elevating subgenera *Xerochlamys* and *Mediusella* Cavaco of *Leptolaena* to independent generic rank (Table 3). However, this elevation of the subgenus *Mediusella* to generic rank was not validly published until Hutchinson's correct combination in 1973. Goldblatt and Dorr (1986) further published the same combination with a more direct reference to the place of valid publication of the basionym. Hutchinson's error by giving a secondary bibliographic citation does not invalidate his publication based on Article 33.3 of the *Code* (Greuter et al., 1994), rendering Goldblatt and Dorr's combination superfluous.

Previous hypotheses of relationships among genera in the Sarcolaenaceae are varied and often conflicting. Capuron (1970), by his own observations and the previous work of Straka (1963), recognized four taxonomic groupings in Sarcolaenaceae (Tables 5 and 6). The first group proposed by Capuron (1970) comprises *Xyloolaena* Baill., *Sarcolaena*, and *Leptolaena* sensu lato (including *Xerochlamys* and *Mediusella*), all genera with a well-developed involucre with one to two flowers at anthesis. The second and third groups each contain a single genus, *Schizolaena* Thouars and *Rhodolaena* Thouars, respectively. *Schizolaena* shares many characters with the first group but differs in its small, simple, ericaceous-type pollen tetrads, which Straka (1963) referred to as pollen type I. *Rhodolaena* has the same pollen type as group 1 but has a reduced involucre at anthesis. Group 4 contains *Eremolaena* Baill., *Perrierodendron* Cavaco, and *Pentachlaena*

Table 5. Generic relationships within Sarcolaenaceae as proposed by Straka (1963).

Group 1	<i>Schizolaena</i> <i>Rhodolaena</i> <i>Eremolaena</i> <i>Sarcolaena</i> <i>Leptolaena</i> <i>Pentachlaena</i> <i>Xyloolaena</i> <i>Perrierodendron</i>
Group 2	
Group 3	
Group 4	

H. Perrier, which all have type III pollen (Straka, 1963). Type III pollen is characterized by discontinuous ridges beside the aperture forming triangles, with each connecting the polar regions of three grains of the tetrad. Genera of Sarcolaenaceae can be distinguished by the following key, modified from Capuron (1970).

KEY TO THE GENERA OF SARCOLAENACEAE

- 1a. Seed with abundant endosperm; seminal integument formed by 2 distinct layers.
 - 2a. Involucre partially or completely enclosing flower buds and well developed at anthesis.
 - 3a. Flower buds partially enclosed in the involucre; ovules more than 4 per locule *Xyloolaena*
 - 3b. Flower buds completely enclosed in the involucre; ovules (1–)2(–4) per locule.
 - 4a. Stipules fused into a single sheath; inflorescence bracts fused.
 - 5a. Leaves with induplicate prefoliation traces; ovules 2 per locule *Sarcolaena*
 - 5b. Leaves without induplicate prefoliation traces; ovules 2(–4) per locule *Xerochlamys*
 - 4b. Stipules free from one another; inflorescence bracts free.
 - 6a. Stamens numerous; ovary 3–5-locular with (1–)2–3 ovules per locule; pericarp of fruit ± lignified *Mediusella*
 - 6b. Stamens 10; ovary 3-locular

Table 6. Generic relationships within Sarcolaenaceae as proposed by Capuron (1970).

Group 1	<i>Xyloolaena</i> <i>Sarcolaena</i> <i>Xerochlamys</i> <i>Mediusella</i> <i>Leptolaena</i>
Group 2	<i>Schizolaena</i>
Group 3	<i>Rhodolaena</i>
Group 4	<i>Pentachlaena</i> <i>Eremolaena</i> <i>Perrierodendron</i>

- with ovules 2 per locule; pericarp of fruit thin *Leptolaena*
- 2b. Involucre not enclosing flower buds and reduced at anthesis.
- 7a. Calyx with only 3 sepals *Schizolaena*
- 7b. Calyx with 5 sepals (2 external and reduced) *Rhodolaena*
- 1b. Seed without or with very reduced endosperm; seminal integument without distinct layers.
- 8a. Ovary 5-locular with 4–6 ovules per locule *Pentachlaena*
- 8b. Ovary 2–3-locular, with 2 ovules per locule.
- 9a. Sepals persistent; ovary 3-locular; fruit dehiscent *Eremolaena*
- 9b. Sepals caducous; ovary 2-locular; fruit indehiscent *Perrierodendron*

SYSTEMATICS OF SARCOLAENA

In his book *Histoires des végétaux recueillis dans les îles australes d'Afrique*, Du Petit-Thouars (1806) described *Sarcolaena*. This genus had previously been called *Tantalus* in an unpublished manuscript by Ferdinand de Norohna, a Spanish botanist who worked in the eastern rainforest of Madagascar (Du Petit-Thouars, 1806). Later, the French botanist A. L. de Jussieu used the name *Eriocarpus*, referring to the hairy character of the involucre, but did not publish it because Thouars convinced him that there were more distinctive characters (Du Petit-Thouars, 1806). Thouars's publication was the first valid description of *Sarcolaena*, which means fleshy, exterior tunic or covering, referring to the involucre. Thouars initial description of *Sarcolaena* included three species: *S. multiflora*, *S. eriophora*, and *S. grandiflora*.

All studies of the genus beyond basic morphology, such as pollen (Carlquist, 1964), wood anatomy (Outer & Schutz, 1981), bark anatomy (Outer & Vooren, 1980), floral morphology (Koechlin, 1972), cytology (Goldblatt & Dorr, 1986), and chemistry (Gaydou & Ramanoelina, 1983) have been parts of broader familial surveys. These have been generally based on generic representatives with few species from *Sarcolaena*. As an example, Goldblatt and Dorr (1986) reported chromosome numbers in *Sarcolaena* ($2n = 22$) but for only the species *S. oblongifolia* and *S. multiflora*. The most recent systematic treatment of *Sarcolaena* is that of Cavaco (1952a). However, according to our observations, the characters that he used to delimit species vary continuously, especially for species with overlapping geographic ranges. Despite Capuron's (1970) proposal that *Sarcolaena* might be only a single variable species, currently available morphological evidence, such as leaf size, number of stamens, and involucral indumentum, supports Cavaco's conclusion that the genus, although varying more or less

continuously over a climatic and geographical continuum, does consist of discontinuous populations that can be recognized as distinct species. This morphological variation in *Sarcolaena* is best represented by recognizing eight species, one of which was recently described.

Cavaco (1952a) cited only 28 collections, as opposed to the 210 cited in the present study. This enhanced number of collections for study makes possible a more precise circumscription of morphological variation of species, with the realization that some characters previously assumed to be constant do vary over the geographic range of a species. For example, *S. multiflora* Thouars, previously characterized by only a single pair of prefoliation traces may, in fact, have from one to three. This variable pattern of leaf traces has also been demonstrated in *S. grandiflora* Thouars and *S. oblongifolia* F. Gérard.

DISTRIBUTION AND ECOLOGY

Madagascar is generally considered to be divisible into two major phytogeographic regions (Perrier de la Bâthie, 1921; Humbert, 1927; Koechlin et al., 1974). These Eastern and Western Regions are further subdivided into several domains. Four Eastern domains consist of: eastern, central, high mountains (>2000 m), and the Sambirano. Two Western domains occur: the western and southern. *Sarcolaena*'s distribution is restricted to three Eastern domains, namely eastern, Sambirano, and central (Fig. 1).

The eastern domain ranges from the coast to about 800 m and from Vohémar in the north to Tolagnaro in the south, and covers almost the entire eastern coast (Fig. 1). Five species, *S. multiflora*, *S. grandiflora*, *S. eriophora*, *S. delphinensis* Cavaco, and *S. humbertiana* Cavaco, occur here, and all except *S. eriophora* are endemic.

The Sambirano domain in northwestern Madagascar is included in the Eastern Region because of climatic affinities (Perrier de la Bâthie, 1921; Humbert, 1927; Koechlin et al., 1974). The range of *S. codonochlamys* Baker is essentially confined to this Sambirano domain with possible extensions slightly north or east (e.g., *Eaux et Forêts Tamatave 66* [P]).

The central domain is an uneven plateau ranging from 800 to 2000 m. Its northern limit is the foot-hills of Tsaratanana, and it extends south to the Isalo plateau. Three species occur in this domain: *S. eriophora* in the central part (Ankazobe) and close to the eastern edge (Anjozorobe); *S. oblongifolia* on western and southwestern slopes between




Figure 1. Phytogeographic subdivisions of Madagascar.

1500 and 2000 m; and *S. isaloensis* A. Randriana-solo & J. S. Mill. confined to the Isalo region.

Species of *Sarcolaena* occur in a great diversity of habitats. These vary from very humid, wet areas without a dry month (rainfall 2000–3500 mm per year) to areas where the dry season lasts for 5–6 months (rainfall 1000–1500 mm per year) (Griffiths & Ranaivoson, 1972; Koechlin et al., 1974). Populations range from the lowland to high elevational sites (1500–2000 m). *Sarcolaena* occurs in evergreen forests on lateritic soil, littoral forests on sand, or sclerophyllous forests on rocky substrates where water and nutrients are quite limited. The wide variation in habitats may account for the vast differences in phenotypic expression present in a taxon. Among and within species, many morphological characters vary continuously, perhaps reflecting edaphic and climatic variation. Populations of *Sarcolaena* in wet, lowland areas tend to have large leaves with few hairs on the abaxial surface, while those in dry areas have smaller, more pubescent leaves. Tree size also decreases with increasing elevation and decreasing rainfall. The most extreme case is the geographically isolated population of *S. isaloensis* at Isalo, where individual plants display very reduced leaves less than 6 cm long and very pubescent involucres.

Species of *Sarcolaena* also occupy an important place in Malagasy vegetation. *Sarcolaena multiflora* and *S. grandiflora* are the most common canopy constituents in eastern coastal littoral or sublittoral forests. On the western slopes of the central domain, at an altitude between 800 and 1600 m, *S. oblongifolia* is the second dominant species after *Uapaca bojeri* Baill. (Euphorbiaceae/Uapacaceae) in Tapia forests. *Sarcolaena oblongifolia* has a tremendous resistance to fire, a yearly occurrence in this part of the island. More interestingly, our field observations indicate that it even outcompetes *U. bojeri* because it is the only woody species that persists in some areas of the Itremo mountain chain that have been severely and repeatedly burned (Fig. 2A).

Griffiths and Ranaivoson (1972) recognized two seasons in Madagascar: the summer (rainy and hot) starting in November and ending in April, and the winter (cool and dry) from May to October. The least rainfall and the lowest temperatures in the eastern domain occur from August through October. Cavaco (1952b) speculated a relationship between rainfall, temperature, and flowering time for *Sarcolaena* species. He stated that species growing in the eastern and Sambirano domains, such as *S. multiflora*, *S. eriophora*, *S. delphinensis*, *S. grandiflora*, *S. codonochlamys*, and *S. humbertiana*, flow-

ered during the driest months with lowest temperature. Species such as *S. oblongifolia* and *S. isaloensis* from the central domain flowered during the last three months of the rainy season. While our field observations and study of herbarium specimens indicate that Cavaco's predictions appear generally accurate, there are clearly exceptions, e.g., *Randrianasolo* 233 is *S. oblongifolia* flowering in early July, and not October or November. This anthesal variation may happen as annual climatic fluctuations occur with species flowering opportunistically.

No information has been previously recorded about pollination or dispersal of *Sarcolaena* species. Now, our field observations suggest these species are pollinated by small to medium-sized bees. Some flower structures suggest bee pollination as evidenced by bright coloration of the corolla, numerous stamens, and especially a floral disk with copious nectar. Further pollination study is needed for a better understanding of this group.

MORPHOLOGY

HABIT

Species of *Sarcolaena* are all densely branched trees, with more or less conic crowns. Tree height ranges from 3 to 20 m, varying according to local climatic and edaphic conditions and thus having little utility as a taxonomic character. For example, *S. oblongifolia* stands only 3–6 m tall at col de Tapia sites between Antsirabe and Ambositra. However, in Ingalo forest, a much wetter region, these trees reach 15 m in height (Morat 3172 & 3323).

LEAVES

Sarcolaena has alternate, simple, entire leaves. Blades are smallest in *S. isaloensis* (2.5–5.3 cm long, 0.5–1.1 cm wide) and largest in *S. multiflora* (8.5–15.5 cm long, 3–6.5 cm wide). Leaf length and width are quite variable within species and can only be used to separate species when blade sizes do not overlap. Leaf shape in *Sarcolaena* also varies. In most species, leaves vary from lanceolate or narrowly elliptic to elliptic, narrowly ovate, or ovate, even oblanceolate in *S. delphinensis* or obovate in *S. eriophora*. Leaves are borne on canaliculate, sericeous petioles that range from 4 to 20 mm. Leaf texture is coriaceous. Pairs of traces lie on each side of the midribs due to induplicate prefoliation (Figs. 2B, 3A). These traces are unique to *Sarcolaena* in the family, although *S. isaloensis* appears not to have them. The number of pairs of



Figure 2. Photos documenting vegetative and floral morphology of *Sarcolaena*. —A. *S. oblongifolia* as a dominant woody species in the Itremo region. —B. Inflorescence and leaves of *S. multiflora*. —C. Inflorescence with opened and unopened flowers of *S. multiflora*. —D. Flower and involucres of *S. oblongifolia*.

these traces ranges from 0 to 4 and is sometimes useful for species recognition. In all species, leaf surfaces are sericeous with T-shaped hairs. There are usually fewer hairs on adaxial surfaces. Abaxial surfaces are also always covered by stellate scales. However, the density and presence or absence of hairs on leaves are variable characters and therefore of limited diagnostic value.

INFLORESCENCES

Inflorescences in *Sarcolaena* are terminal or sub-terminal, dichotomously branched cymes with up to 30 flowers (Fig. 2B, C). This fertile axis may be reduced to a solitary, axillary flower in *S. humbertiana*. Capuron (1970) observed that small-flowered species had more flowers per inflorescence and that large-flowered species generally had fewer. We did

not conduct a quantitative study to confirm or refute Capuron's conclusion; however, we did observe that flower number is generally too variable to be of much use in delimiting species.

INVOLUCRES

Involucre as considered here was defined by Capuron (1970) as a structure distinct from the perianth of the flower (Fig. 2D). It is not a receptacle as implied by Cavaco (1952a, 1952b). However, careful anatomical study is necessary to determine the homologous nature of the involucre in *Sarcolaena*. The involucre surrounds a single flower and is well developed at anthesis. This is in contrast to some genera of Sarcolaenaceae such as *Xyloolaena*, *Rhodolaena*, *Pentachlaena*, *Eremolaena*, and *Perrierodendron*, in which the involucre may subtend

more than one flower or remain reduced at anthesis. Involucral size varies in *Sarcolaena*, ranging from 5–7 mm long and 5–6 mm wide in *S. multiflora* to 7.5–12 mm long and 8–11.5 mm wide in *S. grandiflora*. Involucral shape also varies from widely to very widely obovoid. The involucre consists of two distinct parts with the body or lower portion and the top or upper part divided into separate teeth at anthesis (Fig. 3B, C₁). The involucre is covered by brown to light brown hairs of variable length. In species descriptions, short hairs are defined as less than 1 mm long, and long hairs are longer than 1 mm. Hairs on involucres of *Sarcolaena* vary in shape, length, and orientation and result in four types of indumentum (Stearn, 1992): (1) *sericeous*—with > 1 mm long, appressed, straight, silky hairs; (2) *setaceous*—with > 1 mm long, appressed, straight, thick, bristle-like, dense hairs; (3) *hirsute*—with > 1 mm long, erect, straight, dense hairs; (4) *spreading hairs*—with > 1 mm long, spreading, curved hairs.

CALYX

Terminology describing aestivation follows that of P. F. Quer (1953). The calyx of *Sarcolaena* is dialysepalous with three equal sepals, which are abaxially brown and have long appressed hairs forming apical tufts (Fig. 3C₂). Sepals are membranaceous, contorted, and occasionally imbricate. An exception is *S. humbertiana*, which was reported to have five unequally sized sepals (2 small and 3 large) (Cavaco, 1952a, 1952b). Sepals are always included within the involucre. Sepal shape varies from ovate to very widely or widely depressed ovate, and size ranges from 2 to 8 mm long and 1.5 to 5 mm wide. The length and width of sepals vary continuously within and among species, but these measures can be used to separate species when variation ranges do not overlap.

COROLLA

All species of *Sarcolaena* have a 5-merous, white or yellow corolla (Fig. 2D). The petals are free, obovate, narrowed at the base, glabrous, membranaceous, contorted, and range in size from 12 to 23 mm long and 6 to 15 mm wide. As with the sepals, variation in size is useful in delimiting some taxa.

NECTARY

All species of *Sarcolaena* have an annular and toothed nectary located between the stamens and the corolla (Fig. 3C₂). It secretes a limpid sticky liquid, which probably is an attractant to pollinators.

STAMENS

Stamen number varies considerably throughout the Sarcolaenaceae. It ranges from 5 to 10 in *Leptolaena* (*sensu stricto*) to 80 to 100 in *Perrierodendron* Cavaco (1952a). In *Sarcolaena*, stamens are numerous and may be diagnostic of certain species: *S. delphinensis* has 23 to 28 stamens; *S. multiflora* has 30 to 40. All other species have more than 40. Anthers in *Sarcolaena* are dorsifixed, introrse, and bithecate dehiscing by longitudinal slits. They are approximately the same height as the corolla but generally shorter than the style. Filaments are glabrous, slender, and twisted at their bases (Fig. 2D).

POLLEN

The pollen of Sarcolaenaceae is shed in tetrahedral tetrads. Three major types of pollen have been recognized in the family by Straka (1963, 1964, 1971, 1975) and Carlquist (1964). However, a more recent study by Nilsson and Randrianasolo (1999) suggested four types of pollen. According to Nilsson and Randrianasolo (1999), Type I is the *Schizolaena*-type and includes the genus *Schizolaena* with small (25–40 µm) and simple tetrads, tricolporate or porate pollen grains with the tectum varying from scabrate to verrucate, rugulate, or foveolate. Tetrads of *Schizolaena*-type also lack raised ridges. Type II is the larger *Sarcolaena*-type (75–120 µm), which includes *Sarcolaena*, *Leptolaena*, *Rhodolaena*, and *Xyloolaena*. Here, pollen grains have a smooth tectum with very distinct, thick and continuous ridges. Type III corresponds to the *Eremolaena*-type. This includes only *E. rotundifolia* (F. Gérard) Danguy and presents relatively simple tetrads ca. 70 µm in diameter. Type IV, or the *Perrierodendron*-type, is defined as large tetrads (45–90 µm) with a smooth tectum and is known from *Pentachlaena*, *Perrierodendron*, and one of the two species of *Eremolaena* (*E. humblotiana* Baill.). The tectum of this last type also is characterized by raised, discontinuous ridges. While pollen morphology has proven useful for elucidating generic relationships, *Sarcolaena* species all share Type II pollen with only slight structural differences. Hence, pollen is of little use for delimiting species or elucidating relationships within *Sarcolaena*.

GYNOECIUM

The ovary in *Sarcolaena* is superior, trilocular, usually with two pendulous ovules in each locule, and is covered with long, reddish brown hairs (Fig. 3C₃). The single style is as long as or slightly longer than the petals, ranges from 7 to 24 mm long, and

is terminated by a trilobed, discoid stigma (Fig. 2D). Style lengths can be used to separate some species.

FRUIT

Sarcolaena fruits are indehiscent capsules with a very fragile pericarp. They are completely enclosed in the involucre in all species except *S. delphinensis*, in which they are only partially included. Fruit size ranges from 5 to 10 mm long and 5.5 to 9 mm wide, and due to extensive variation and overlap has little utility in distinguishing species. Each fruit contains 3 to 6 black, rugose seeds to 3–5 mm in length.

SYSTEMATIC TREATMENT

Sarcolaena Thouars, Hist. Veg. Isles. Austral. Afric. 37. 1806. TYPE: *Sarcolaena multiflora* Thouars (lectotype, designated by Bullock (1960)).

Sarcochlaena orth. var. in Spreng., Linn. Syst. Veg. Vol. II, 594. 1825.

Trees, (3–)8–15 m tall, usually branched. Leaves alternate, simple, the blade petiolate, entire, coriaceous, persistent, with well-marked longitudinal traces from induplicate prefoliation (except in *S. isaloensis*) and brochidodromous venation. Stipules deciduous, leaving circular scars on the young twigs. Inflorescence terminal or subterminal, cymose, ± dichotomously branched in most species, but in *S. humbertiana* reduced to solitary flowers in terminal or axile position. Flowers pedunculate, each with a cup-shaped, hairy, generally brown involucre; calyx dialysepalous, the 3 sepals (5 in two whorls in *S. humbertiana*) widely ovate, contorted, membranaceous, brown, sparsely sericeous with an apical tuft of long, simple hairs on the abaxial surface, always enclosed in the involucre; corolla 5-merous, widely obovate, contorted, dialypetalous, membranaceous, white, white-yellow, or white-blue; nectary annular, toothed, borne between the corolla and the stamens; stamens 23 to 61, slightly exserted, the filaments unequal in length, slender, glabrous, the anthers dorsifixed, introrse, bithecate, parallel, dehiscing by longitudinal slits; ovary oblong, pubescent, trilocular with 2 pendulous ovules per locule, the placentation axillary, the style ± exserted. Fruits capsular with a very fragile pericarp in maturity, enclosed completely in the transformed involucre, except in *S. delphinensis* where they are partially enclosed.

Distribution. *Sarcolaena* is endemic to Madagascar and occurs primarily in the Eastern and

Central phytogeographic regions with disjunct occurrence in the Sambirano domain, considered part of the Eastern Region because of similar climatic conditions and corresponding forest composition and profile (Koechlin, 1972).

No holotype was designated by Thouars in the original generic description, and Bullock (1960) designated *Sarcolaena multiflora* as the lectotype of the genus from the three species described by Thouars: *S. multiflora*, *S. grandiflora*, and *S. eriophora*.

Vernacular names. The Malagasy language varies from one part of the island to another, and different vernacular names are used for *Sarcolaena*. Those recorded with collections are reported here with an indication of their region: helana or mera (East coast), vondrozona (Central), and hazo atambo (Northwest). There is no indication of vernacular recognition of different species.

Uses. There are no detailed ethnobotanical studies of *Sarcolaena*. The species are reputed to have hard wood that is good for building houses, and they are also commonly used as fuelwood along the east coast. *Sarcolaena oblongifolia*, with its attractive flowers, has been cultivated in the Parc Botanique et Zoologique de Tsimbazaza for about ten years; the aesthetic beauty of *Sarcolaena* species makes them candidates as ornamental plants in tropical areas.

KEY TO THE SPECIES OF SARCOLAENA


1a. Leaves less than 1.1 cm wide 6. *Sarcolaena isaloensis*

1b. Leaves more than 1.1 cm wide.
2a. Stamens 23–28; fruit partially enclosed in the involucre; leaves oblanceolate 2. *Sarcolaena delphinensis*

2b. Stamens 30 or more; fruit completely enclosed in the involucre; leaves generally narrowly ovate, narrowly elliptic, or lanceolate.
3a. Hairs of the involucre dense and more than 1 mm long.
4a. Erect and spreading hairs found on the involucre; leaf apex obtuse or sometimes mucronate 3. *Sarcolaena eriophora*

4b. Only spreading hairs on the involucre; leaf apex acute to attenuate or slightly acuminate 5. *Sarcolaena humbertiana*

3b. Hairs of involucre not dense, less than 1 mm long.
5a. Style greater than 16 mm long; petals more than 12 mm wide.
6a. Style 18–24 mm long; sepals 6–8 mm long; petals 20–23 mm long; leaves 3.2–9.2 cm long; involucre widely obovate,



- ± top-bottom compressed —— 8. *Sarcolaena oblongifolia*
6b. Style 16–17 mm long; sepals 4–5 mm long; petals 16–21 mm long; leaves 8–13.5 cm long; involucre very widely obovate, cup-shaped —— 4. *Sarcolaena grandiflora*
5b. Style less than 16 mm long; petals less than 12 mm wide.
7a. Abaxial leaf surface ferruginous; stamens 43–61; sepals 4.5–5.5 mm long —— 1. *Sarcolaena codonochlamys*
7b. Abaxial leaf surface not ferruginous; stamens 32–39; sepals 2.5–3 mm long —— 7. *Sarcolaena multiflora*

1. *Sarcolaena codonochlamys* Baker, Bull. Misc. Inform., CCXCII, 11. 1893. TYPE: Madagascar. North Madagascar: Without exact locality, *Baron* 6366 (holotype, K not seen; isotype, P!).

Trees, 8–15 m tall, the young twigs sericeous, glabrate. Leaf blades lanceolate, sometimes narrowly oblong, (6)8–11(–16.5) cm long, (2)2.2–3.5(–5.3) cm wide, apex acute, narrowing to an acuminate, mucronate or sometimes retuse apex, base obtuse, rarely acute; adaxial blade surfaces glabrous, sometimes with long appressed hairs along the midrib (more so on young leaves), abaxial blade surfaces ferruginous, sparsely sericeous, with 1 or 2 induplicate prefoliation traces on either side of midrib; petiole sericeous, canaliculate, (6)7–10(–12) mm long. Inflorescence terminal, 4- to 16- or more flowered. Involucre widely to very widely obovate, (5)7–8(–10) mm long, (6)7–8(–9) mm wide, exterior surface with short brown hairs, inside sericeous; sepals widely to very widely ovate, 4.5–5.5 mm long, 4–5 mm wide, the abaxial sepals with a few long hairs with apical tuft; petals obovate, 16–20 mm long and 9–10 mm wide, glabrous, white or blue; stamens 43 to 61, 15–18 mm long, with anthers small, 1 mm long; ovary hairy, oblong, 1.5–2 mm long, style 12–15 mm long, glabrous. Fruit 9–10 mm long and 7 mm wide, enclosed in an involucre 13–15 mm long and 11–12 mm wide.

Sarcolaena codonochlamys is distinct in having lanceolate leaves abaxially ferruginous.

Distribution and ecology. *Sarcolaena codono-*

chlamys has been collected in the Sambirano, in northwestern Madagascar, particularly around Ambanja and Ambilobe. It also occurs near Rantabe in the eastern rainforest (Fig. 4).

Additional specimens examined. MADAGASCAR. **Antsiranana:** Marovato Ambanja, close to Mabibo village, 72 D 309 (P); S of Ambilobe, Decary 14837, 14799 (P); Plateaux of Ankarana, near Ambondrofe, Humbert 18945 (P); Sambirano basin and Zangoa, less than 500 m high, Perrier de la Bâthie 3026 (P); vicinity of Ambilobe, Perrier de la Bâthie 3033 (P); Bas Sambirano, Perrier de la Bâthie 15676 (P); Tandavan'i Galoka (Chaine du Galoka), SW of Ambilobe, NE end of ridge, 5 km along road from Beramanja, Phillipson 2014 (MO, TAN); S of Ambanja, N slope of the Ambatomenavava peak, 500 m, RN [Ramarokoto and Ratoto] 1448 (P); Antanimandry, county of Beramanja, Ambilobe district, SF 3515 (P); Ampondrabe, Ambanja, SF 5838 (P); Bekaka, Benavony, Ambanja, SF 7504, 9296 (P); Andampy, Ambilobe, SF 10432 (P); Ankotika Ambanja, SF 10641 (P). **Mahajanga:** Bejofo, Maromandia district, Decary 939, 2221 (P); hills in Andranosamonta vicinity, Analalava district, Perrier de la Bâthie 3022 (P). **Toamasina:** Ambodisira, Rantabe, Randriamanga 139 (P). **Province unknown:** N Madagascar without exact locality, Baron 5816, 6380 (K, P); Decary 14795 (TAN).

2. *Sarcolaena delphinensis* Cavaco, Bull. Mus. His. Nat. (Paris) Ser. 2, 22: 615. 1950. TYPE: Madagascar. Toliara: vicinity of Fort-Dauphin, 1–25 m, 20 Sep.–6 Oct. 1928 (fl), Humbert 5996 bis (holotype, P!).

Trees, 8–10 m tall, densely branched; young twigs sericeous, later glabrous. Leaf blades oblanceolate, 5–9 cm long, 1.2–3 cm wide, apex acute and often abruptly acuminate, less commonly mucronate or retuse, base acute to cuneate; adaxial blade surfaces with sparsely appressed hairs, usually glabrate with age, abaxial blade surfaces sericeous, with 1 or 2 induplicate prefoliation traces on either side of midrib; petiole (6)7–9(–10) mm long, adaxially canaliculate, brown sericeous. Inflorescences terminal, 4- to 16- or more flowered. Involucre widely obovate, 6–7 mm long, 4–5 mm wide, the interior surface setaceous, the exterior surface brown, showy with medium-sized appressed hairs; sepals 3 mm long, 2 mm wide, free, these generally contorted in opened flowers but sometimes imbricate in the buds, sparsely sericeous on abaxial surfaces with apical tufts; petals obovate, 1.2–1.5 cm long, 0.5 cm wide, glabrous, white to yellow; stamens 23–28, 1.2–1.5 cm long, attached



Figure 3. —A. Inflorescence branch of *S. multiflora*. —B. Unopened floral involucre of *S. grandiflora*. —C. *S. oblongifolia*: —C₁. Unopened and opened flowers. —C₂. Flower outside the involucre. —C₃. Cross section of involucre with young fruit.

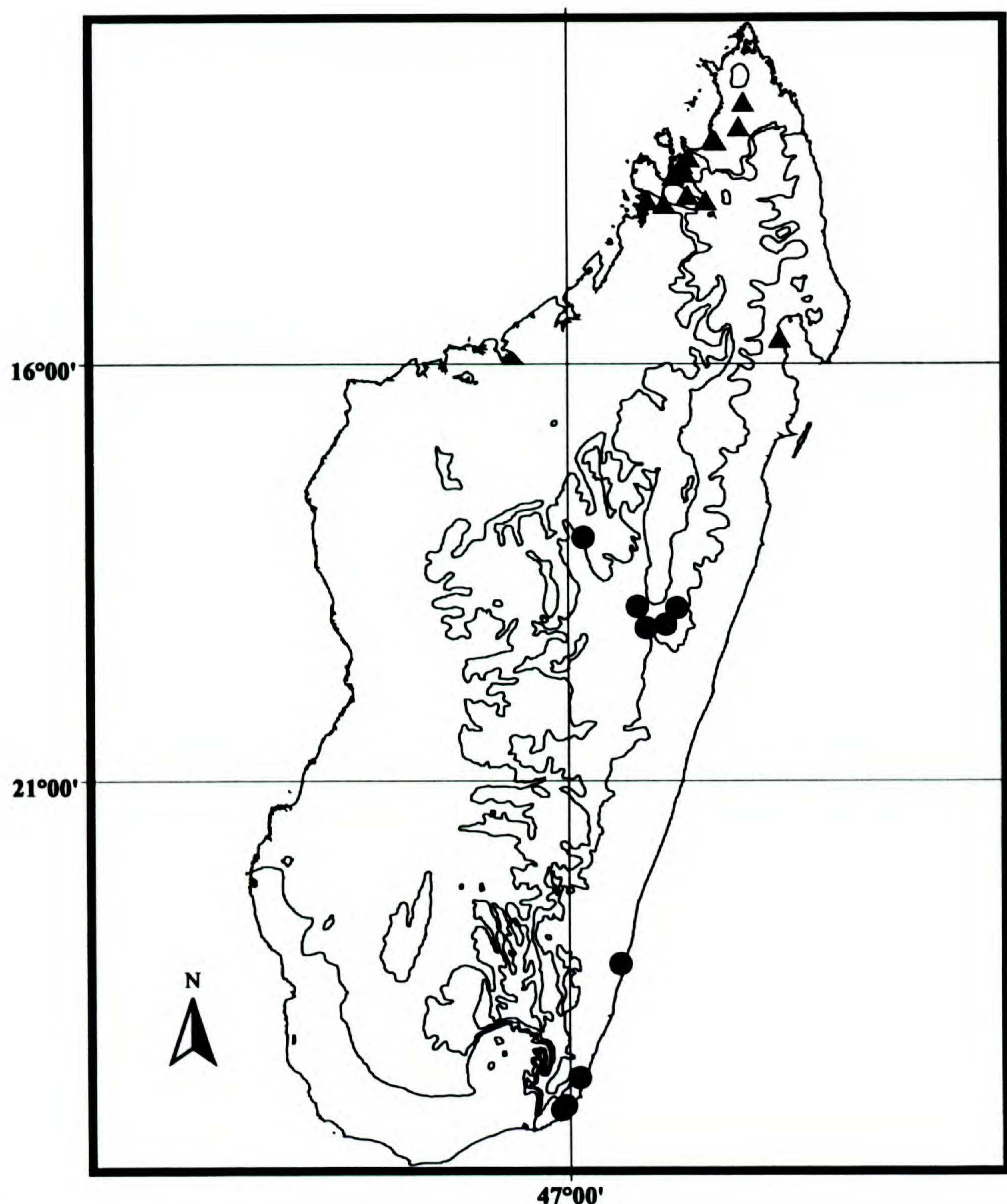


Figure 4. Geographic distribution of *Sarcolaena codonochlamys* (triangles) and *S. eriophora* (circles).

between ovary and nectary, anthers 0.8–1 mm long; ovary ± oblong, 1.8–2 mm long, very hairy, style 8–10 mm long, glabrous. Fruit ovoid, 11–12 mm long, 8–9 mm broad, incompletely included in the brownish green, very widely obovoid involucre, 8–9 mm long, 11–11.5 mm broad.

Sarcolaena delphinensis is distinctive because its fruits are only partially enclosed in the involucre, and its leaves are oblanceolate in shape. It has also 23 to 28 stamens, the fewest of any species.

Distribution and ecology. This species occurs in moist sublittoral forest from sea level to 200 m

and is only known from southeastern Madagascar, in the vicinity of Tolagnaro (Fort-Dauphin) (Fig. 5).

Additional specimens examined. MADAGASCAR. To- liara: environs de Fort-Dauphin, *d'Alleizette* 1182 (P); environs de Fort-Dauphin, 1–25 m, *Humbert* 5996 bis (P); Fort-Dauphin region, N of the town along trail following pipes to town's water source, forest called Lakandava, 100–200 m, *McPherson et al.* 14894 (A, MO, P, TAN); Fort-Dauphin Lakandava, bassin du JIRAMA, just close the pipes back to town, 50–70 m, *Randrianasolo* 256 (K, MO, P, TAN); vicinity of Fort-Dauphin, 2 km W of Man- antantely, *Randrianasolo* 278 (K, MO, P, TAN).

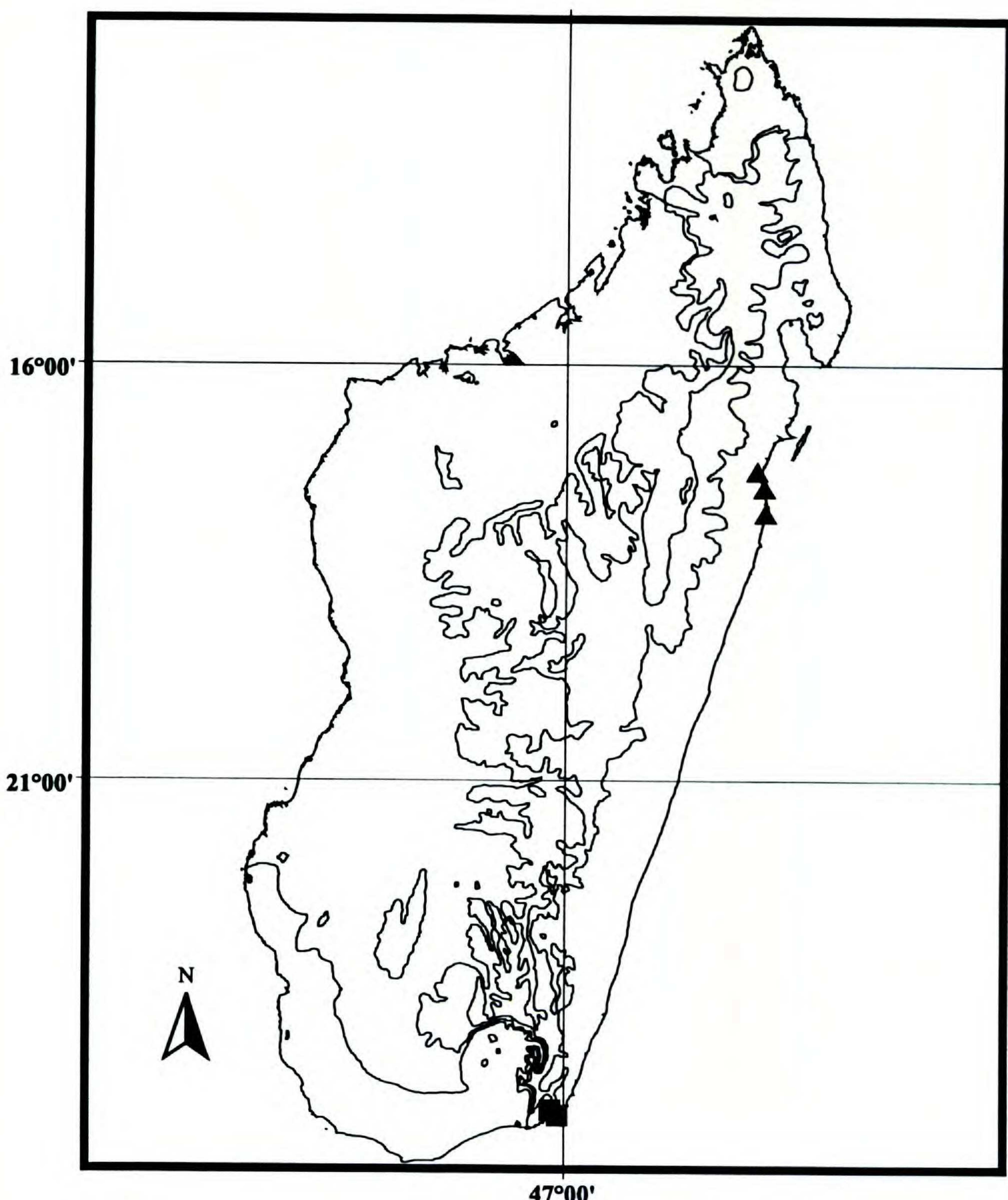


Figure 5. Geographic distribution of *Sarcolaena delphinensis* (squares) and *S. grandiflora* (triangles).

3. *Sarcolaena eriophora* Thouars, Hist. Veg. Isles Austral. Afriq. 40. 1806. TYPE: Madagascar. Without exact locality, *Commerson s.n.* (holotype, P!).

Trees, 3–10 m tall; twigs sericeous, more so in young branches. Leaf blades variable in shape, narrowly ovate, sometimes narrowly obovate or narrowly elliptic to ovate or obovate, (3.9–)4.7–6.8(–8.4) cm long, 1.7–4.3 cm wide, apex usually obtuse, sometimes mucronate, base obtuse; adaxial blade surfaces sparsely sericeous along the midrib, more so in younger leaves, but sometimes glabrous, ab-

axial blade surfaces sericeous, with none or one induplicate prefoliation trace on either side of midrib; petiole (6–)7–9(–12) mm, adaxially canaliculate, brown and sericeous. Inflorescence terminal, with 1 to 7 flowers per inflorescence. Involucrum very widely obovate, 8–9 mm long, ca. 8 mm wide, hirsute on the lower part and sericeous on the upper part, the interior surface sericeous; sepals very widely ovate, 4–5 mm long and 4 mm wide, with a few long appressed hairs on abaxial surface, and an apical tuft of hairs at the apex; petals 14–15 mm long and 5–6 mm wide, glabrous; disk 1 mm

high, yellow; stamens 44 to 47, unequally sized, 6–7 mm long, the anthers very small, 0.5–1 mm long; ovary very hairy, ± 2 mm long, style 7–12 mm long, pubescent from the base to ca. $\frac{2}{3}$ of its length. Fruit widely ovoid to widely depressed ovoid, 5–7 mm long and 5.5–6 mm broad, included within involucre 10–11 mm long and 9–11 mm broad.

The most distinctive feature of *Sarcolaena eriophora* is differentiation between hairs on the lower and upper portions of the involucre. On the lower part the hairs are dense and erect, but on the upper part they are less dense and spreading. This species also has the narrowest petals in the genus.

Distribution and ecology. *Sarcolaena eriophora* occurs in wet littoral forests on sand along the southeast coast of Madagascar, from Fort-Dauphin to Farafangana (Fig. 4). It also occurs from the pre-montane forests along the escarpment between the eastern domain and the central domain to the plateau.

Additional specimens examined. MADAGASCAR.
Antananarivo: Ankazobe, Canton Maridaza, Réserve Spéciale Ambohitantely, RN [Jean de Dieu] 190 (P), SF 9594, 14684, 18008, 18358, 19875 (all P); Station Forestière Mandraka, 1210 m, SF (Rakotorazaha) 1903 (P); Station Forestière Mandraka, vallée de la Mandraka, vers PK 69, SF 18502 (P). **Fianarantsoa:** Cote-Est, près de l'embouchure du Faraony, Perrier de la Bâthie 3013 (P); Farafangana, coastal forest of Nosiala, SF 16210 (P). **Toamasina:** Ampitanonoka, entre Ampitanonoka et Sahalampona, 1200 m, Cours 2629 (P); Mangoro, entre Beparasay et Moramanga, 800 m, Perrier de la Bâthie 17201 (P); Moramanga, Analamazaotra-Périnet Réserve Spéciale, SF 10347, 14961, 15019, 19081 (all P); Moramanga, Niagara, Sarindreniny, Toby P.K 27 route d'Anosibe, SF 25802 (P). **Toliara:** Fort-Dauphin, Petriky, Forêt littorale sur sable de Petriky, derrière les lacs, Allorge 798 (MO); Fort-Dauphin region, NE of city, in region called Mandena, beyond the botanical garden and QIT camp, in forest remnants near coastal lake, 25 m, McPherson & Dumetz 14319 (MO, TAN); Fort-Dauphin, forestry station of Mandena, 12 km of Fort-Dauphin, Randrianasolo 252, 254 (K, MO, P, TAN); Mandena 12 km N of Fort-Dauphin, forest on sand, SF 6088, 7010 (P); Bemangidy forest, N of Mahatalaky, 100 m, SF 11782 (P); sandy dunes in Mandromondromotra, N of Fort-Dauphin, SF 22644 (P); about 10 km NNE of Fort-Dauphin, Mandena region, coastal low forest on sand, 10 m, Zarucchi et al. 7602 (MO, P, TAN).

4. *Sarcolaena grandiflora* Thouars, Hist. Veg. Isles Austral. Afriq. 40. 1806. TYPE: Madagascar. Without exact locality, Thouars 806 (lectotype, selected here, P!; isolectotype, P!).

Trees, 8–15 m tall; young twigs light brown sericeous, glabrate with age. Leaf blades lanceolate to narrowly ovate or ovate, 8–13.5 cm long, (2.5)–3–4.6(–5.5) cm wide, apex acute to slightly acuminate, base obtuse; adaxial blade surfaces generally gla-

brous but occasionally with very few appressed long hairs, abaxial blade surfaces brown, more so in young leaves, sparsely sericeous, with 1 to 4 induplicate prefoliation traces on either side of midrib; petiole 8–15 mm long, adaxially canaliculate, brown sericeous, more so on young leaves. Inflorescences terminal, (4)–10–11(–16)-flowered. Involucre very widely obovate, 7.5–12 mm long, 8–11.5 mm wide, the interior surface setaceous, exterior surface with very short brown hairs; sepals ovate to widely ovate, 4–5 mm long and 3.5–6 mm wide, glabrous but with a tuft of hairs at the apex; petals obovate, 16–21 mm long and 14–15 mm wide, glabrous, white; stamens 46–50, filaments unequal in size, 15–19 mm long, anthers 1–1.2 mm long; ovary oblong, 2.5 mm long, with dark red-brown hair, style 16–17 mm long, pubescent from the base to $\frac{2}{3}$ of its length. Fruit completely enclosed in a depressed obovoid involucre, 9–11 mm long, 17–19 mm broad.

Sarcolaena grandiflora is easily distinguished from other members of the genus by its very widely obovate cup-shaped involucre (Fig. 3B) and the presence of pubescence on the lower $\frac{2}{3}$ of the style.

Distribution. This species has been collected in only two areas of Madagascar (Fig. 5). It occurs in the wet, central and eastern littoral and sublittoral forests in the northern part of Toamasina province, in the vicinity of Fénérive-Est.

Additional specimens examined. MADAGASCAR.
Toamasina: Tampolo, 10 km from N of Fénérive-Est, road to Soanieran'Ivongo, just at the intersection with the road to Rantolava, over the bridge, Randrianasolo 244 (K, MO, P, TAN); Botanical garden #21, Tampolo, Fénérive, SF 16455, 19176, 19228 (P, TEF); littoral forests on sand, in Antetezana, N of Tamatave, SF 18089 (P, TEF); sublittoral forests on sand in Mahambo, S of Fénérive, SF 18147, 18149 (P, TEF).

5. *Sarcolaena humbertiana* Cavaco, Bull. Soc. Bot. France, Actual. Bot. 97: 96. 1950. TYPE: Madagascar. Toliara: Manampanihy basin (Sud-Est), Mont Vohimavo N of Ampasimena, 830 m, 27–28 Mar. 1947 (fl, young fr), Humbert 20705 (holotype, P!).

Trees, 3–4 m tall; twigs brown sericeous, glabrate. Leaf blades lanceolate to narrowly elliptic-oblong, 5.5–9.3 cm long, 1.9–3 cm wide, apex acute to attenuate or slightly acuminate, base obtuse; adaxial blade surfaces glabrous, occasionally with a few appressed hairs on midrib, abaxial blade surfaces sparsely brown sericeous, with one induplicate prefoliation trace on either side of midrib; petiole 6–7 mm long, adaxially canaliculate, brown sericeous. Flowers solitary, axillary or terminal. Involucre ± 12 mm long, exterior surface sericeous,

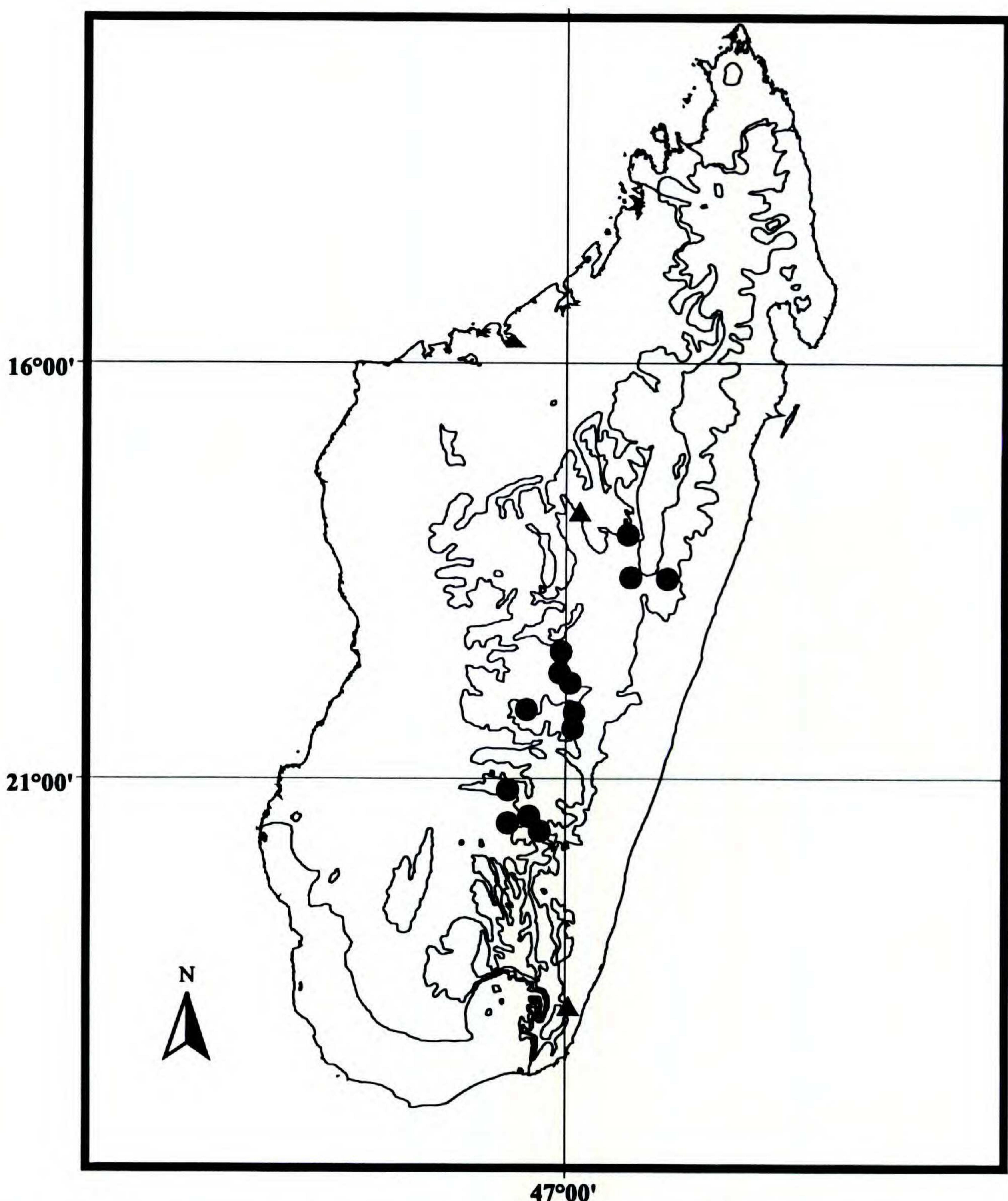


Figure 6. Geographic distribution of *Sarcolaena humbertiana* (triangles) and *S. oblongifolia* (circles).

interior surface pubescent; calyx 5-merous, with 2 exterior and 3 interior sepals, exterior sepals ovate, 2 mm long and 1.5 mm wide, with few hairs at the apex, inner sepals widely to very widely ovate, 4 mm long and 3.5–4 mm wide, sparsely sericeous with an apical tuft of hairs; corolla 5-merous; stamens about 40; ovary hairy. Fruit unknown.

Despite the fact that few collections have been made for *Sarcolaena humbertiana*, it appears that the involucre not divided into two parts separates it from the rest of the species in the genus. According to Cavaco (1952), the character of solitary

flowers bearing 5 instead of 3 sepals is unique in the genus. However, the number of specimens is not sufficient to confirm whether Cavaco's description was accurate.

Distribution. This species has been collected only twice, at Ambohitantely at 1600 m, north of Ankazobe, in the province of Antananarivo; and distantly in southeastern Madagascar, to the north of the Fort-Dauphin region, at the Vohimavo peak at 830 m (Fig. 6).

Additional specimen examined. MADAGASCAR. **Antananarivo:** Tamponketsa au Nord d'Ankazobe (centre),

forêt d'Ambohitantely et restes de forêts aux alentours, 1600 m, *Humbert 11098 bis* (P).

6. *Sarcolaena isaloensis* A. Randrianasolo & J. S. Mill., Novon 4: 292–294. 1994. TYPE: Madagascar. Fianarantsoa: plateau and valleys of Isalo, W of Ranohira, 800–1250 m, 29 Jan.–2 Feb. & 8–10 Apr. 1955 (young buds), *Humbert 28695* (holotype, P!).

Trees, 6–10 m tall; young twigs sericeous, glabrate. Leaves alternate, simple, entire, coriaceous; leaf blades narrowly ovate to narrowly elliptic, 3–5.3 cm long, 0.5–1.1 cm wide, apex acute, mucronate, base obtuse; adaxial blade surfaces glabrous, abaxial blade surfaces sparsely brown sericeous, lacking induplicate prefoliation traces; petiole 4–8 mm, canaliculate, abaxially brown sericeous. Inflorescence terminal, flowers solitary or paired. Young involucre surrounded by a brown sericeous caducous spathe. Involucre with long, spreading, stiff hairs, peduncle brown sericeous, 2–6 mm long. Flowers and fruits unknown.

This species is distinctive in its very narrow leaves that lack the induplicate prefoliation traces present elsewhere in *Sarcolaena*, and in the long, stiff, spreading hairs on the young involucre.

Distribution and ecology. This species occurs in Isalo, west of Ranohira, the southern limit of the central domain (Fig. 7).

Specimens examined. MADAGASCAR. **Fianarantsoa:** Isalo massif, Betanimanga, 1000–1300 m, 18–20 Nov. 1960, *Leandri 3951* (P); Isalo, tapia woodland, 900 m, 24 Nov. 1932, *Perrier de la Bâthie 16688* (P); Isalo massif nearby the sign of Isalo Sud, W of Ranohira, SF 11.675 (P).

7. *Sarcolaena multiflora* Thouars, Hist. Veg. Isles. Austral. Afriq. 40. 1806. TYPE: Madagascar. Without exact locality, *Thouars s.n.* (lectotype, here designated, P!; isolectotype, P!).

Sarcochlaena multiflora var. *latifolia* Hochr., in Annuaire Conserv. Jard. Bot. Genève, 12: 73. 1908. TYPE: Madagascar. District of Vatomandry, en sol sablonneux, arbre de taille moyenne, 25 Oct. 1903, *Guillot 52* (G).

Trees, 4–15 m tall; young twigs brown sericeous to glabrate with white lenticels. Leaf blades lanceolate to ovate or narrowly elliptic to elliptic, (5.5–)8.5–15.5(–19.7) × (2.5–)3–6.5(–8.5) cm, apex acute to obtuse, sometimes rounded and abruptly acuminate, mucronate or retuse, base obtuse, rounded or subcordate; adaxial blade surfaces generally glabrous but occasionally with a few

long, appressed hairs along the midrib, more so on young leaves, the abaxial surface sparsely sericeous, very often on the midrib only, with 1 to 3 induplicate prefoliation traces on either side of midvein; petiole (9–)10–15(–20) mm long, adaxially canaliculate, sericeous. Inflorescence terminal, usually 20- or more-flowered, but sometimes less. Involucre widely to very widely obovate, 5–7 mm long and 5–6 mm wide, exterior with short hairs, inside surface sericeous; sepals very widely to very depressed ovate, 2.5–3 mm long and 3–4 mm wide, with a few long, appressed hairs on the abaxial surface and with an apical tuft of hairs; petals obovate, 12–18 mm long and 6–10 mm wide, glabrous, white or yellow; stamens 32 to 39, 11–13 mm long, anthers 1 mm long; ovary hairy, 1.5–1.8 mm long, style 10–14 mm long, basally pubescent. Fruit very widely ovoid, 6–7 mm long and 6–7 mm broad, completely included in mature involucre 7–9 mm long and 6–11 mm wide.

Sarcolaena multiflora shares many morphological characters with *S. grandiflora* and can also be confused with *S. oblongifolia*. However, it is easily distinguished from these two species by its small involucres, its large leaves up to 20 cm long, inflorescences usually with 20 or more flowers, each with 32 to 39 stamens (Figs. 2C, 3A).

Distribution and ecology. This species is the most widespread in the genus. It ranges from the northeast to Fort-Dauphin in both rainforest and littoral forests of the eastern domain (Fig. 7).

Additional specimens examined. MADAGASCAR. **Antsiranana:** Sambava, Forêt d'Atiala, 100 m, *Deroin et al. 138* (MO, P); Environs de Sambava, massif rhyolitique d'Ambatobiribiry, 50–345 m, *Humbert et al. 24429* (P); Antalaha Ambohitralanana, RN 3385 (P); Antalaha, RN 4928 (P); Antalaha Ambohitralanana, RN 5719, 6794, 8054, 10098, 10740 (all P); Antalaha, SF 1646 (TAN); Sambava, eastern forests, remnant forests in SW Sambava vicinity, SF 9244 (P); Manampona Tsaratanana, SF 9477 (P); Anovoka Sambava, SF 13285 (P). **Fianarantsoa:** Mananjary, *Geay 8087* (MO); Ambalavonika Mananjary, *Geay 8088, 8089* (P); Anefitrala Vangaindrano, SF 4091 (P); Mananjary, SF 5629 (P); Andrianabo-Amparibe Vangaindrano, SF 7109 (P); Nosiala-Efatsy Farafangana, SF 7297 (P); Pangalana Sud, Mananjary, SF 9504 (P); Nosiala-Efatsy Farafangana, SF 12212 (P); Fitiamito ambahy Nosy Varika, SF 13457 (P); Amborondamba Nosy Varika, SF 15478 (P); Farafangana, Bema Evato, SF 15242 (P); Tohakandra Ihorombe Farafangana, SF 16154 (P); Marohita Mananjary, SF 16176, 21001 (P). **Toamasina:** Vatomandry, *Bernard 1903* (P); Ile Sainte Marie, *Bernier 191* (P); Ambila Lemaitso, *Boiteau 457* (P), *Boivin s.n.* (P); Foulpointe, *Bojer s.n.* (P); Ambila Lemaitso, derrière la lagune, 3–5 m, *Cours 2940* (P); along the route #5, S of Fénérive-Est between PK 80–PK 100, mostly sandy soil, more than 50 m, *Croat 32592* (MO); road to Analalava, W of Foulpointe, *Dorr & Barnett 3317* (MO, P), 4459 (MO); littoral forest at Reserve of Mahatsara Foulpointe,

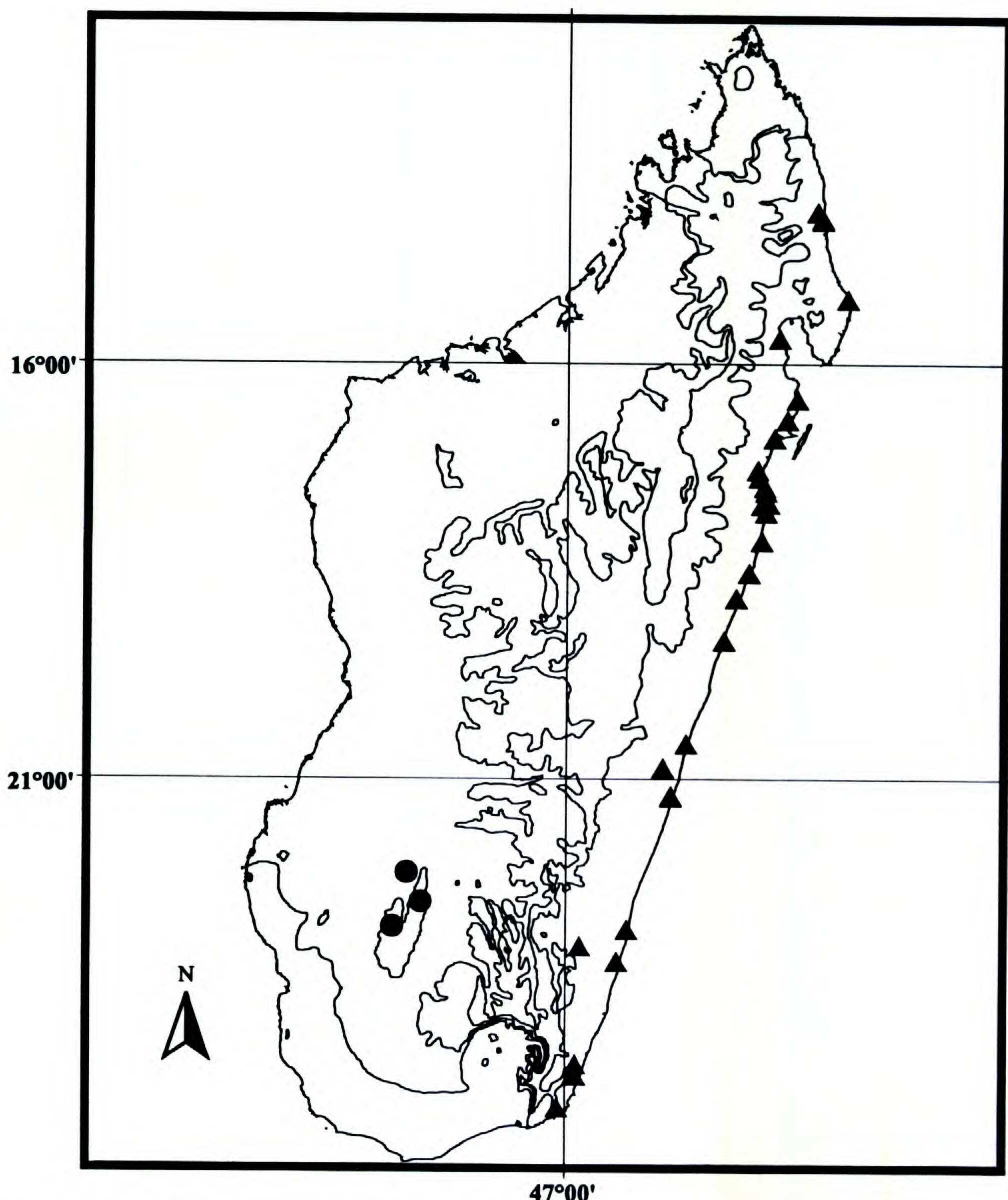


Figure 7. Geographic distribution of *Sarcolaena isaloensis* (circles) and *S. multiflora* (triangles).

Evraud 11267 (MO); Circa Tamatave, Goudot s.n. (P); Vatomandry, Guillot 52 (G, MO); Soanieran'Ivongo, Humbert 3160 (TAN); 1 km W of Ambila Lemaitsos, Keating & Miller 2249 (MO, P, TAN); Soanierana, Lam & Meeuse 5579 (K, P); Environs d'Ambila Lemaitsos, Le Thomas 124 (P); about 2 km W of town on road toward Rantabe (RN5), partially cleared coastal forest along road on sandy soil, Lowry II et al. 3994 (MO); Tampina, Martine D8 (P); 1 km NW of Ambila Lemaitsos, Miller & Schatz 3637 (MO, P, TAN); Antanambe Mananara, Morat et al. 8626 (P); Foulpointe, Peltier 3364 (P); Fénérive-Est, Perrier de la Bâthie 3001 (P); Tampina, Perrier de la Bâthie 13265, 15873 (P); Mahanoro, Perrier de la Bâthie 18118 (P); Antanambe Mananara, Raharimalala 137, 259 (P); Manompana, route de Mananara, Rakotozafy 1318 (TAN); Ambila

Lemaitsos, close to the ferry, 5 km S of the Ambila Lemaitsos village, Randrianasolo 223 (K, MO, P, TAN); vicinity of Foulpointe, along the road RN 5, Randrianasolo 245 (K, MO, P, TAN); Eastern domain, Ambila Lemaitsos, 10 km E of Brickaville, coastal dune forest and taller forest behind lagoon, Schatz & D'Arcy 1484 (MO); Ambila Lemaitsos, coastal dune forest just N of railroad bridge, W of Pangalane (canal), Schatz et al. 3442 (MO, P); Ambila Lemaitsos, SF 1107 (P, TAN), 1618 (MO, P, TAN), 5868, 8310 (P); Antetezana Tamatave, SF 1324, 14496 (P); Soanierana Ivongo, SF 2415 (P); Antananala Ambila Lemaitsos, SF 3221 (P, TAN); Ambodisira Rantabe Maroantsetra, SF 6250 (P); Tampolo Fénérive Est, SF 10054, 10834, 15162, 15337, 16456, 17803 (P); Iamboala Mahanoro, SF 11108 (P); Sahavolamena Soanierana Ivongo,

SF 12417 (P); sublittoral forests on sand in Mahambo, S of Fénérive Est., *SF 18148* (P); vicinity of Antongil Bay, littoral and sublittoral forests on sand in Antoraka, *SF 18279* (P); Tampina, *Ursch 118* (P); vicinity of Tamatave, *Viguier & Humbert 282* (P). **Toliara:** Fort-Dauphin, *Closel 143* (P); forestry station of Mandena, 7 km N of Fort-Dauphin, forest on white sand, elev. 10 m, *D'Arcy & Rakotozafy 15383* (MO); littoral forest, Fort-Dauphin, *Decary 10144* (P); forest glade, Evatra cap Fort-Dauphin, *Decary 10889* (P); Ebakika, ancient dunes Fort-Dauphin, *Decary 11077* (P); Mandena Fort-Dauphin, forest on sand, *Dorr 3996* (MO), *Dumetz 706* (MO, P); St. Luce forest Fort-Dauphin, *Dumetz et al. 746* (MO); Mandena station 9 km NE of Fort-Dauphin and less than 1 km W of Lac Ambavarana, *Gereau & Dumetz 3266* (MO); 5.5 km E of Fort-Dauphin-Manantenina road, on road to Manafiafy, in dense coastal forest, *Gereau 3422* (MO); Mandena, *Johnson s.n.* (MO, P); between St. Louis Peak and the sea, Fort-Dauphin vicinity, *Humbert 5996* (P, TAN); region of Fort-Dauphin, on QIT concession, Mandena site, low forest on sand, *McPherson et al. 14136* (MO); St Luce (Manafiafy), 44 km N of Fort-Dauphin on road to St Luce, dense coastal forest on flat sandy substrate, 50 m, *Phillipson et al. 3959* (MO); Mandena, in the Botanical garden, *Randrianasolo 251, 253* (K, MO, P, TAN); Mandena, *SF 394* (P), *1547* (P, TAN), *3385* (TAN), *4046* (P, TAN), *6250, 7009, 7815, 14535, 15621* (P); Bemangidy Manantenina Fort-Dauphin, *SF 21446* (P); about 10 km NNE of Fort-Dauphin, Mandena region, coastal low forest on sand, *Zarucchi et al. 7505* (MO, TAN). **Province unknown:** central Madagascar, specimens without exact locality, *Baron 4650* (P); *Baron s.n.* (P); *Boivin s.n.* (P); *Chapelier s.n.* (P); *Commerçon s.n.* (P); *Cours 2940* (P); *Humblot 163, 165* (P), *169* (TAN), *365* (P); *Goudot s.n.* (P); *Lantz 7* (P); *Perrotet s.n.* (P); *Richard s.n.* (P); *Waterlot s.n.* (P).

8. *Sarcolaena oblongifolia* F. Gérard, Ann. Inst. Bot. Geol. Colon. Marseille, ser. 3, 7: 26–28. 1919. TYPE: Madagascar. Fianarantsoa: Tapia woodland, rocky (quartzitic), between Ambatomainty and Itremo, Ambositra, 1400 m, June 1912 (fl), *Perrier de la Bâthie 3006* (holotype, P!).

Trees, 3–12 m tall; young twigs sericeous, glabrate. Leaf blades narrowly ovate, elliptic or oblong to ovate or elliptic, (3.2–)4.6–7.4(–9.2) cm long, apex acute, sometimes obtuse, mucronate or retuse, occasionally acuminate, base ± obtuse; adaxial blade surfaces glabrous, occasionally with a few long appressed hairs, more so when young, with 1 or 2 induplicate prefoliation traces on either side of midrib; petiole (5–)7–10(–11) mm long, adaxially canaliculate, brown sericeous. Inflorescence terminal, reduced dichotomous cymes of 1 to 2 or 4 flowers. Involucre widely obovate, 10–13 mm long and 9–10 mm wide, exterior surface brown with short hairs, interior sericeous; sepals widely ovate, 6–8 mm long and 4.5–5 mm wide, abaxial surface with few appressed long hairs and an apical tuft of hairs at the apex; corolla obovate to widely obovate, 20–23 mm long and about 13 mm wide, white to

slightly yellow, glabrous; stamens 45 to 50, filaments ca. 16–18 mm, anthers 1–1.1 mm long; ovary oblong, 2–2.2 mm long, style 18–24 mm long, pubescent from the base to ca. ⅔ of its length. Fruits completely included in the involucre, which is 13–15 mm long and 13.5–24 mm wide.

Sarcolaena oblongifolia is one of the most distinctive species of the genus. It can be easily recognized by its large flowers having sepals 6–8 mm long and petals 20–23 mm long (Figs. 2D, 3C₂).

Distribution and ecology. This species occurs mainly on the central and southwestern slopes of the central domain where it is one of the main components of the sclerophyllous forests from Antsirabe, south to Ihosy, and west to the Itremo chain (Fig. 6). Its distribution extends also to the eastern escarpment (from ca. 800 m), a transitional zone between the central and eastern domains.

Additional specimens examined. MADAGASCAR. **Antananarivo:** 5 km of Antilarisona N of Antsirabe, 1250–1300 m, *Croat 29205, 29228* (MO, P); rocky hillside along route #35, 54 km E of Finandrohana, area very dry with occasional springs, 1300 m, *Croat 29652* (MO); Parc Tsimbazaza, Antananarivo city, cultivated, *Dorr 2746* (MO); Anjozorobe, ca. 2 km E of Primary and Secondary Antsahabe School at Anjozorobe, primary mountain top, mesic forest, slightly disturbed, 1410 m, roadside, *Harder et al. 1542* (MO, P); 7 km E of Anjozorobe, transitional zone between plateau and eastern domain, slightly disturbed wet forest, 1450 m, *Lowry II et al. 4389* (MO, P, TAN); 8 road-km along track W of Anjozorobe, 3.4 km past school near Antsahabe, Mt. Hafatraeo, disturbed remnant forest, 1270 m, *Zarucchi et al. 7371, 7546* (MO, P, TAN). **Fianarantsoa:** Col d'Itremo, 2 km of Vodiharana, 1600 m, *Baum 29* (MO); Col de tapia, patches of the western slope forests, *Boiteau 332* (P); Col des Tapias, route d'Ambositra, *Boiteau 332 B* (P); between Antsirabe and Ambositra, PK 202, 1400 m, *Bosser 9958* (P, TAN), *Service forestier 231P* (P); PK 12 road Ivato to Ambatofinandrahana, *Bosser 9959* (P, TAN); Mont Ibity (W slope), SW of Antsirabe, 1900 m, *Cremers 2036* (MO, TAN); Ambositra district, Andina Ihadilalana county, Ambatonanahary montane, 1400–1800 m, *Cours 5737* (P); vicinity of Ambatofinandrahana, 1600–1800 m, *Decary 13208* (P); Faliarivo Ambositra, western forest, *Decary 14026* (P); Ambositra in the tapia woodland, *Decary 17250* (P); Ambatofinandrahana, tapia woodland forest, *Decary 17416* (P); between Antsirabe and Ambositra, PK 202, 1400 m, *Dorr 3840* (MO); Itremo, 1800 m, *Guillaumet 4257* (P, TAN); vicinity of Ambositra, rest of western slope woodland in Faliarivo, 1600 m, *Humbert 14485* (P); montanes W of Itremo, 1500–1700 m, *Humbert 28271, 30022* (P); Itremo, Massif d'Itremo, W of Ambositra, dry rocky slopes with scattered trees, 1500 m, *McPherson et al. 16464* (MO); Itremo, *Morat 899* (P, TAN); Ingalo forest, western slope formation, *Morat 3172* (TAN), 3323 (MO, P, TAN); district Ambositra, near Anjoma, tapia woodland forest, *Peltier 2191* (P); Fiadanana, Ilaka centre, *Peltier 2163* (P); tapia woodland forest, 1600 m, *Perrier de la Bâthie 9339* (P); western slope formation, S of Antsirabe, 1500 m, *Perrier de la Bâthie 13095* (P); Mont Ibity, 2000 m, *Perrier de la Bâthie 13575* (P); Andringitra chain, 1500

m, *Perrier de la Bâthie* 13915 (P); tapia woodland, S of Iby, 1200 m, *Perrier de la Bâthie* (P, TAN); half way Antsirabe–Ambositra, RN 7, PK 45, Col de tapia, *Randrianasolo* 226 (K, MO, P, TAN); road to Ambatofinandrahana, 12 km from Ivato, *Randrianasolo* 231 (K, MO, P, TAN); road to Morondava, 8.7 km SW of Ambatofinandrahana, *Randrianasolo* 233 (K, MO, P, TAN); Itremo chain, 43 km from Ambatofinandrahana, along the road to Morondava, *Randrianasolo* 236 (K, MO, P, TAN); Ambatofinandrahana–Mandrosonoro, Pk 19.3, *Randrianasolo* 238 (K, MO, P, TAN); between Antsirabe and Ambositra, Pk 202, 1400 m, SF 231 (P); Ankaramena Ambalavao, SF 1918 (P); Antanimena forest, SF 4724 (P); Amboandrozana forest, Ambalavao Ankaramena, SF 10528 (P); rest of forest of western slope, forest of Faliarivo, SW of Ambositra, SF 11544 (P); Ankijoma-Ambohimahazo-Ambositra SF 13471, 14767 (P); Centre, granitic massif of Ifandana, between Ankaramena and Ihosy, 1300–1400 m, SF 23507 (P). **Toamasina:** Antatabe, 20 km E of Mandraka on the road to Moramanga, 900 m, disturbed premontane forest, *Miller et al.* 6275 (MO, P, TAN); Analamazaotra, forest N of Andasibe, 860 m, along the railroad tracks, *Miller et al.* 8745 (MO, P, TAN); Ambatovy, 11 km NE of Moramanga, Morat 3223 (MO, P).

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